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Peter J. Mahoney
Utah State University

Julie K. Young
Utah State University, julie.k.young@aphis.usda.gov

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Uncovering behavioural states from animal activity and site fidelity patterns

Peter J. Mahoney[1]* and Julie K. Young[2,3]

[1]*Department of Wildland Resources and The Ecology Center, Utah State University, Logan, UT 84322, USA;* [2]*USDA-WS-NWRC-Predator Research Facility, Logan, UT 84322, USA; and* [3]*Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*

Summary

1. Space use by animals has important implications for individual fitness. However, resource requirements often vary throughout the course of a lifetime and are a reflection of the demands associated with daily tasks or specific life-history phases, from food acquisition to reproduction, and emphasize the need to classify resource selection relative to specific behavioural states. Site fidelity is often indicative of behaviours important for individual maintenance (e.g. foraging), species' life history (e.g. seasonal site selection), social communication (e.g. scent-marking) and species interactions (e.g. predation, competition). Thus, resolving site fidelity patterns associated with key behaviours is essential to accurately quantify behavioural-dependent resource needs and the fitness consequences of space use.

2. We propose a novel method for identifying site fidelity patterns in animal location data using a convex hull clustering program called R Animal Site Fidelity (rASF). We also provide a means of integrating activity as a measure of behavioural state. We demonstrate the utility of the approach in identifying cougar (*Puma concolor*) predation events, coyote (*Canis latrans*) den and rendezvous sites, and coyote territorial boundaries.

3. We parameterized rASF based on site fidelity characteristics that best characterized the clustering behaviour of interest and estimated behavioural state from either dual-axial accelerometer data or movement trajectory statistics. When behaviour was used in conjunction with cluster-specific metrics (duration, proportion of diurnal fixes and landscape composition), we could accurately predict prey species associated with cougar kills and differentiate pup-rearing from scent-marking sites in coyotes.

4. Site fidelity patterns and activities associated with animal revisitation will be key to identifying the behavioural motivations behind observed patterns of space use. Our approach provides an efficient, rigorous and repeatable means of identifying site fidelity patterns associated with specific behavioural states without the need for direct observations, which are often impossible to collect at large spatial scales and in dense habitat. As such, this framework has significant potential to inform theory in behavioural ecology while providing managers with better resolution on appropriate management targets associated with key aspects of a species' life history.

Key-words: accelerometer, clustering, coyote, denning, GPS, home range, movement, predation, puma, territoriality

Introduction

Understanding the behavioural motivations underlying observed patterns in animal movement is a central theme in behavioural ecology (Nathan 2008). Importantly, animal movement and space use are relevant to an individual's fitness and manifest as the aggregation of behavioural trade-offs made by the organism throughout the course of a lifetime. However, the resource requirements for self-maintenance (e.g. foraging, refuge) and reproduction are often disparate, emphasizing the need to distinguish relevant behaviours when classifying resource selection (Owen-Smith, Fryxell & Merrill 2010; Roever *et al.* 2014; Bouyer *et al.* 2015). Failing to do so can lead to biased expectations of resource use or confound our understanding with regard to the specific resource needs of a species (Roever *et al.* 2014). Further, accounting for behaviour in assessments of resource use is vital to improve our comprehension of selective pressures shaping populations through the demographic consequences of animal space use in changing environments (Tuomainen & Candolin 2011; Johnson *et al.* 2015; Childs, Sheldon & Rees 2016).

However, resolving the link between animal space use and behaviour is limited by our ability to observe individuals in wild settings without measurable observer effects. Advancements in tracking technology have led to decreases in relocation intervals such that animal activity can be inferred from an animal's movement trajectory (Gurarie, Andrews & Laidre 2009; Beyer *et al.* 2013; Gurarie *et al.* 2016). In addition, many tracking platforms are being outfitted with sensors (e.g. accelerometers or gyrometers; Wilmers *et al.* 2015) capable of collecting data on fine-scale directional movement in two or three dimensions and can also be used as a measure of animal

*Correspondence author. E-mail: pmahoney29@gmail.com

activity. Measures of activity are often used to classify behaviour into states or behavioural patterns of extended duration (Martin & Bateson 2007). Thus, activity data, derived from technology or direct observations, are necessary for empirical evaluations of behaviour and can be used in conjunction with animal relocation data (i.e. spatial data) to classify an animal's behavioural state and associated resource utilization (Nams 2014; Abrahms *et al*. 2016).

Ideally, researchers should correlate observed behaviours with recorded patterns in activity through supervised statistical procedures (e.g. Nathan *et al*. 2012; Wang, Nickel & Rutishauser 2015). However, observing wild-type behaviours is difficult to impossible in most systems. Thus, evolving technologies and analytical methodologies will play a key role in permitting researchers to pursue lines of inference related to behavioural motivation and the fitness consequences of animal space use (Wilmers *et al*. 2015). One such alternative is to capitalize on unsupervised statistical techniques for inferring behaviour from sensor-derived activity data. Current unsupervised methods can provide a coarse metric for behavioural state through classification of animal path metrics. Such methods include multistate random walk (Morales *et al*. 2004; Beyer *et al*. 2013) and behavioural change point analysis (BCPA) (Gurarie, Andrews & Laidre 2009; Gurarie *et al*. 2016). While animal trajectories can provide useful insight into an individual's behaviour at a given location, path metrics may be too coarse in contexts where the interval between relocations is prohibitively long, precluding our ability to resolve transitions between behavioural states. In such cases, directional sensor data can help to fill the gaps by providing finer temporal resolution on activity with minimal impacts to hardware battery life (Gao *et al*. 2013). However, only a few unsupervised methods can be extended to evaluate directional sensor data alone or in conjunction with animal relocation data (Nams 2014; Gurarie *et al*. 2016).

In cases where coarse estimates of behavioural state (i.e. resting, moving and foraging) are sufficient, unsupervised statistical methods can be a useful tool for classifying behaviours associated with relevant space use patterns. For example, many species exhibit some level of site fidelity (i.e. clustering), which is often indicative of behaviours important for individual maintenance (e.g. foraging; Wakefield *et al*. 2015), a species' life history (e.g. migration and seasonal site selection; Teesdale, Wolfe & Lowe 2015) and social communication (e.g. scent-marking; Allen, Wallace & Wilmers 2015), as well as community and ecosystem-level processes (e.g. predation; Smith, Wang & Wilmers 2015; Ebinger *et al*. 2016). While identifying behaviours associated with high-fidelity sites may be straightforward in some species (Wakefield *et al*. 2015), for others it is difficult to tease apart which sites are correlated with specific behavioural states using raw relocation data alone. Provided there is sufficient spatial and temporal resolution, behavioural states associated with a given high-fidelity site can be estimated using activity data and one of several unsupervised methods. We can then better inform our assumption of behavioural states associated with site-specific fidelity patterns, while potentially improving our inference and predictions of species-specific behaviour (e.g. predation and reproduction) within the context of site fidelity through time.

We propose a novel method for identifying site fidelity patterns from animal relocation data using a program call R Animal Site Fidelity (rASF). rASF implements a clustering algorithm based on local convex hulls and provides functionality to integrate estimates of activity as derived from trajectory statistics or directional sensor data. Here, we demonstrate the utility of the approach in identifying a range of site fidelity patterns while linking estimated behavioural state derived through unsupervised behavioural change point procedures (Gurarie, Andrews & Laidre 2009) and *k*-means clustering of activity data. We implement three case studies representing a range of plausible site fidelity patterns by resolving the location of (i) predation events (short-term, high intensity of use), (ii) reproductive sites (variable duration, moderate-to-high intensity of use) and (iii) territorial boundaries through conspecific marking sites (long-term, low intensity of use) using a combination of clustering procedures and expected behavioural states associated with the identified locations. In case 1, we use relocation and directional sensor data to identify predation events in mountain lions *Puma concolor*. In case 2, we identify den and rendezvous sites in a strongly territorial species, coyotes *Canis latrans*, using a combination of relocation and directional sensor data. In case 3, we demonstrate how site fidelity can inform our expectations of home range by identifying presumed territorial marking sites of coyotes (Wilson & Shivik 2011), and use associated trajectory-based activity to inform behavioural state of the individuals while at marking sites. rASF can be used to partition data by site fidelity pattern, behavioural state or a combination of fidelity and behavioural state to permit assessments of the associations between landscape composition and site fidelity, as well as variation within and between individuals.

Materials and methods

CLUSTER IDENTIFICATION

The program rASF is coded in R (v.3.2.4; R Core Team 2016) and uses local convex hulls to resolve behavioural clustering events (see 'Data accessibility' below). Users specify four parameters that reflect the desired scale of site fidelity: (i) the minimum number of locations ($N_{total} = 1_{focal} + N_{revisits}$), (ii) the maximum spatial distance between two locations, (iii) the time interval length between locations and (iv) whether to constrain time as within or outside a given interval in order for a point to be included within a cluster. The software loops through every location within a time series, clusters locations that meet the user-defined criteria, draws a convex hull around each individual cluster of points and merges (i.e. unionizes) all hull clusters that overlap in space and time (Fig. 1). These procedures generate cluster-specific utilization distributions located throughout an animal's home range. The output includes cluster-specific data, such as cluster duration, cluster area, number of points and spatial output for use in GIS software, statistical analysis or both. As the number and size of clusters can be sensitive to the parameter inputs, we recommend an evaluation of cluster sensitivity to pre-defined parameters, as well as visual inspection of the output, for a range of parameter

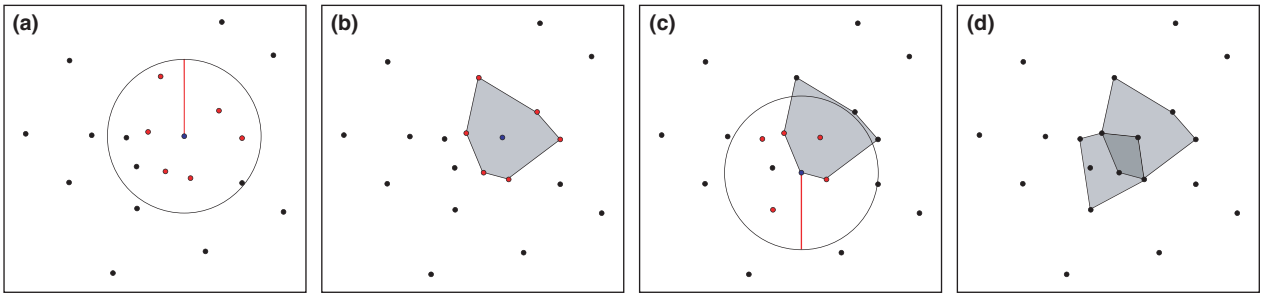

Fig. 1. A schematic of the cluster identification process in chronological order. The process first (a) identifies all points that occur within the spatial buffer (red line) and time interval (red points), (b) identifies the convex hull of 'clustered' points, (c) moves to the next point in the time series and repeats the process and ultimately (d) stacks overlapping polygons (in time and space) into a single cluster.

values (see Appendix S1, Supporting Information). Although not necessary for use with this methodology, rASF incorporates methods that permit integration with activity data, allowing the user to define cluster-specific behaviour qualitatively or empirically.

INCORPORATING ACTIVITY

Raw activity data can be stored in one of several ways: (i) as a single affiliated time series (sensor- or trajectory-based), (ii) as a window of time around a given cluster or point (sensor) or (iii) aggregated activity by points within cluster (sensor- or trajectory-based). The R code we have developed for the rASF (see 'Data accessibility' below) provides an efficient means of integrating cluster output with the BCPA approach described in Gurarie *et al.* (2016) and implemented in the R package *bcpa* (v.1.1; Gurarie 2014). In brief, the BCPA uses a moving window with a user-defined window size to classify a single 'likely' change point – or transition in behavioural state – within each window along an activity time series. Change points are classified using one of eight likelihood models ranked by Bayesian information criterion representing all combinations of mean activity (μ), standard deviation in activity (σ) and characteristic time-scale of autocorrelation (τ) in activity. The characteristic time-scale captures the temporal range of autocorrelation in activity and is dependent on the time interval between measurements (i.e. the unit of time, Gurarie 2014). The window size is effectively a tuning parameter whereby smaller windows permit the estimation of finer-scale transitions in behavioural state. However, Gurarie (2014) recommends a minimum window size of 30 steps, which appears to be the lower limit for model convergence under most scenarios.

Behavioural change point analysis takes a single activity variable stored as a time series and is often a composite metric derived from movement-based statistics. A commonly used, movement-based composite metric is persistence velocity as defined by eqn (1), where V is velocity, or the estimated movement rate, between time $t-1$ and t. θ is the turning angle centred on 0 (vector trajectory from $t-2$ to $t-1$) at time t.

$$V_p = V * \cos(\theta) \qquad \text{eqn 1}$$

We provide a slight extension in rASF to permit greater ease of incorporating activity metrics derived from directional sensor data into BCPA. One recommended composite metric for directional sensor data is the Vector of Dynamic Body Acceleration (VeDBA) defined in eqn (2) (see Qasem *et al.* 2012 for additional details). Variable A is acceleration along the x, y and z axes as measured by directional sensors.

$$\text{VeDBA} = \sqrt{(A_x^2 + A_y^2 + A_z^2)} \qquad \text{eqn 2}$$

Smoothing sensor data along each axis by a running average is often recommend to help account for gravitational bias before analysing directional sensor data (Qasem *et al.* 2012). However, we do not use the raw or composite metrics directly, but instead rely on BCPA outputs which can include a smoother derived from a moving window.

Importantly, directional sensor data can be difficult to manage as quality, quantity and post-processing can vary significantly between hardware manufacturers. It is best to choose the platform (or manufacturer) with the greatest amount of user control over directional sensors if activity data are a priority. However, activity was not of primary concern in the studies presented here; therefore, we utilized the dual-axis accelerometer sensors in our existing GPS collar platforms (i.e. $A_z = 0$ in eqn 2).

CASE-SPECIFIC METHODS AND RESULTS

Case 1: predation – short-term, high-intensity fidelity

We demonstrate how the clustering program can be used to identify predation events with relocation and activity data (directional sensor) derived from movements made by two adult female cougars during 2014 and 2015. The data were from a 4-year study (2012–2015) on Monroe Mountain, Fishlake National Forest in south-central Utah. All cougars were treed using hounds, immobilized with ketamine and xylazine (with weight-dependent doses) and fitted with Lotek GPS collars (Model GPS3300S; Lotek, Newmarket, ON, Canada) containing dual-axis accelerometers following pre-approved animal care protocols (Utah State University IACUC protocol #2182). We programmed all cougar collars to log 5-min averages for X- and Y-directional activities with a 4-h GPS relocation interval. The collars were a store-on-board design, necessitating cougar recapture after a year or more of deployment in order to recover all data. Thus, we often attempted to locate kills made by our study animals 2–18 months after the predation event occurred. The clustering program allowed for rapid batch processing of collar data as soon as collars were in hand, permitting quick turnaround and a list of candidate kill clusters for technicians to investigate. We used a minimum fix count of three relocations, a spatial buffer of 100 m and a temporal buffer of 72 h and included all locations that were within the 72-h time interval. Our biological justifications for these parameter values were the desire to resolve any cluster with a minimal residency of 8 h ($\geq$3 fixes), to identify clusters of points that could accommodate resting sites near predation events ($\leq$100 m based on observations from the field) and to allow residency flexibility over a

Table 1. The total number of clusters identified, number of clusters visited and number of prey by species (values in parentheses are percentages) for two adult female cougars (F53 and F64) on Monroe Mountain, Fishlake National Forest, Utah, during 2014 and 2015

	F53 (%)	F64 (%)
Total clusters	89	109
Visited clusters	35	52
Number of clusters w/Prey	24 (69)	45 (87)
Total prey found	30	53
Number of elk	7 (23)	16 (30)
Number of mule deer	21 (70)	34 (64)
Number of other	2 (7)	3 (6)

rolling window of 72 h based on observed ungulate prey handling times. The number of clusters identified was relatively insensitive to perturbations in these values (Appendix S1). Due to time constraints, crews were only able to visit a random subset of clusters for each individual during the summer of 2015 (Table 1). The species, sex and age of prey were identified where possible.

Next, we integrated activity data as derived from accelerometers by calculating VeDBA and estimating BCPA for the activity time series. We used the change point statistics to classify behavioural state(s) associated with each cluster using *k*-means clustering (Zhang *et al*. 2015). The number of *k*-means clusters was estimated using the R package *NbClust* (v.3.0; Charrad *et al*. 2014), which uses 30 different metrics to assess the appropriate number of clusters for the data. We then used our subset of visited clusters to predict the occurrence of mule deer, elk or other (beaver, *Castor Canadensis*; coyote; domestic sheep, *Ovis aries*; and domestic cattle, *Bos taurus*) prey species using classification-based random forest (R package *party*, v.1.0-25; Strobl *et al*. 2008) with cluster-specific characteristics and BCPA-derived activity as predictors. Cluster-specific characteristics included duration, proportion of nocturnal fixes and cougar ID, as well as landscape features such as elevation (USGS 30-meter DEM, 2010), terrain ruggedness index (Riley, DeGloria & Elliot 1999), distance to shrub cover (≥30%, LANDFIRE 2012), distance to tree cover (≥50%, LANDFIRE 2012) and aspect (cardinal direction).

We visited 87 potential kill clusters and identified a total of 69 prey remains (Table 1). BCPA visualizations of predation clusters were qualitatively distinct between the two primary ungulate prey, mule deer *Odocoileus hemionus* (Fig. 2, fawn and adult in Clusters 10 and 16, respectively) and elk *Cervus elaphus* (Fig. 2, Cluster 18). The timing of points within clusters, the duration of clusters and the activity immediately following cluster initiation appear to be good indications of whether or not a kill occurred at a given site (Fig. 2; Table S1). We were able to identify four behavioural states using the dual-axis accelerometer data, BCPA output (τ_{unit} = 5 min) and *k*-means clustering (Table 2). The first behavioural state is indicative of low activity or resting. States two and three are distinguishable from one another by the characteristic time-scale of autocorrelation, represented by the coefficient τ, and reflect differences in the consistency of movement at moderate levels of activity. Thus, State two may reflect more dynamic movement attributable to reduced duration of autocorrelation at moderate levels of activity (State two: 47·9 min; State three: 142·3 min). However, states two and three are likely reflective of behaviour associated with sustained levels of moderate activity where more directed or rhythmic movements are a component, such as walking and possibly feeding after a kill is made (see below). State four represents higher levels of activity, likely associated with higher rates of travel or hunting.

We could not use random forest to predict the occurrence of predation events using output from rASF as one or more kills were identified at 69 of 87 clusters visited (79·3%), constraining our sample of undetected or non-predation sites. Thus, we limited our assessment to predicting prey species at identified kill sites using site- and cluster-specific characteristics. Even with a relatively small sample of kill sites and low-resolution directional sensor data (i.e. dual-axial vs. tri-axial accelerometer data), random forest maintained 71% accuracy (1 – 'out-of-bag' error) in predicting prey species using 17 predictor variables (Fig. S1). Importantly, the most influential predictor variables included cluster duration and proportion of nocturnal fixes, as well as the SD in VeDBA, median and SD in the time-scale of autocorrelation after cluster initiation (8 h post-initiation), and SD in the time-scale of autocorrelation before cluster initiation (4 h pre-initiation, Fig. S1). Random forest performed well in predicting deer kills (90%; n = 42), moderately well for elk (50%; n = 22) and very poorly for all other species (0%; n = 5; Table S2).

Case 2: reproduction – intermediate fidelity

We further demonstrate the ability to tune rASF to identify sites of moderate-to-high intensity of use over longer periods of time than typically associated with predation events. As an example, we use the clustering software to identify the occurrence, timing and location of denning and rendezvous sites in coyotes. This data set was also derived from the 4-year study (2012–2015) on Monroe Mountain, Fishlake National Forest in south-central Utah. Coyotes were captured using either contracted helicopter net-gunning during the winter or padded leg-hold traps (Victor #3 soft catch) fitted with tranquilizer tab devices (TTDs containing Propriopromazine, Balser 1965) during the remainder of the year. Coyotes were fitted with Lotek GPS collars (Model GPS6000) containing dual-axis accelerometers, which were programmed to log 5-min averages for *X*- and *Y*-directional activities and 6-h GPS fix intervals from the end of August through May and 3-h GPS fix intervals from the June through the end of August. The capture and handling protocols were approved by IACUC (Utah State University IACUC protocol #2182). All individuals were released at the site of capture.

We illustrate the approach with a single reproductive male using a subset of data from March through August of 2014, the time period for pup rearing prior to the initiation of pup dispersal in the Fall (Harrison, Harrison & O'Donoghue 1991; Gese, Ruff & Crabtree 1996). We used a minimum number of five fixes, a spatial buffer of 50 m and a temporal buffer of 10 days, and selected locations that occurred within the specified time interval. Here again, we chose parameter values to help resolve frequent revisitation over the duration of their site-specific use (≥5 fixes), to incorporate clusters of points that could accommodate pup movement or adult bedding sites (<50 m) and to allow flexible but extended residency over a rolling window of 10 days. As with the cougar clusters, the number of clusters identified was relatively insensitive to perturbations in these values (Appendix S1), with the possible exception of the minimum number of fixes. However, we chose an intermediate value of five here to capture short duration rendezvous sites near the end of the summer at the risk of identifying too many sites that were not reflective of pup-caching sites. We integrated activity as described for the predation clusters above.

The output from rASF identified 12 potential pup-rearing sites. The *k*-means clustering diagnostics supported three behavioural states, indicative of low-, moderate- and high-activity levels (Table 2). The natal den (i.e. Cluster 1; Fig. 3) was confirmed through ground-truthing via radio telemetry in late May of 2014. The male remained in the area of the natal den for at least 19 days before the pups were moved *c*.

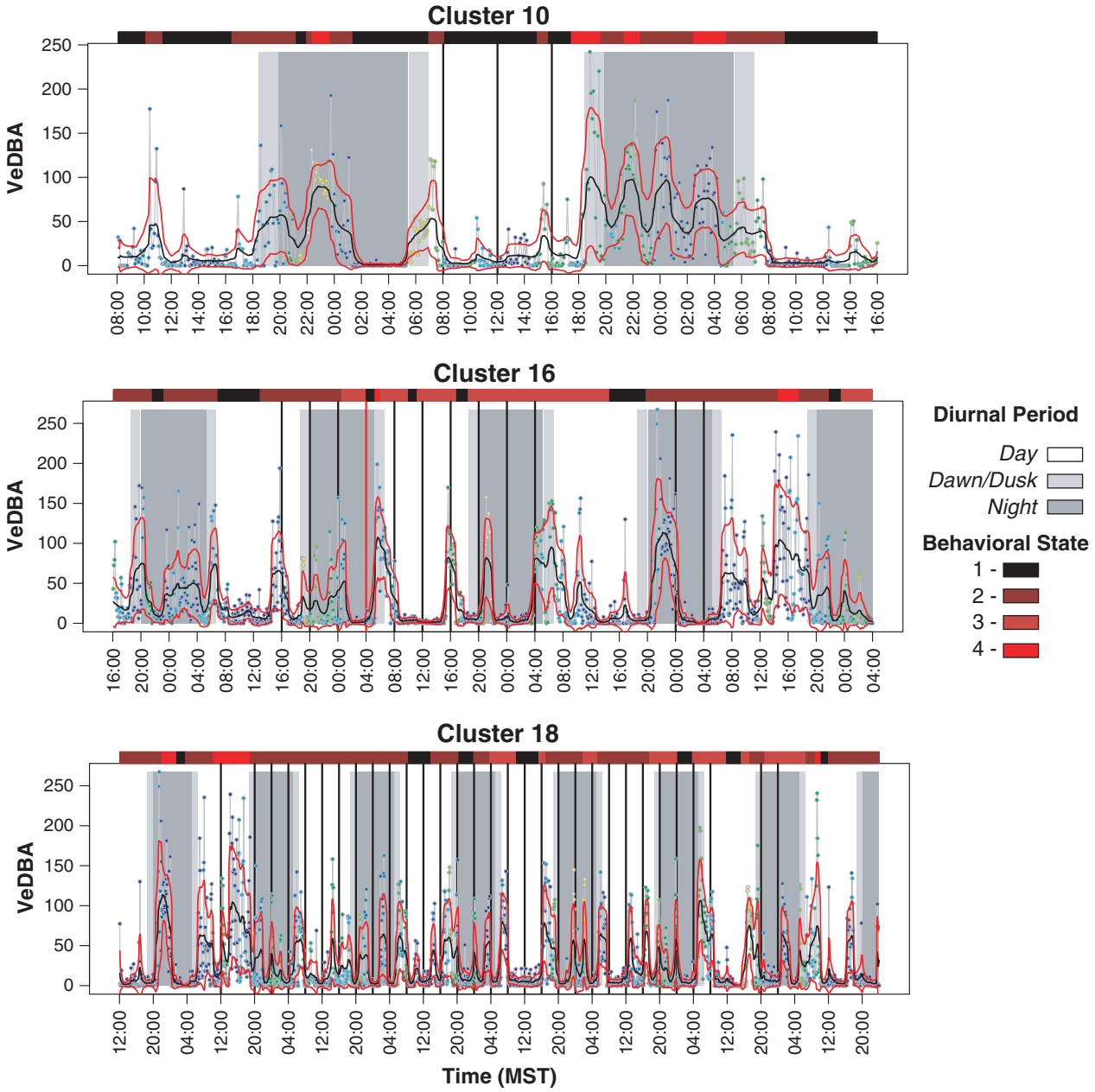

Fig. 2. Three representative clusters derived from GPS relocations of a single female cougar (F53) with a 24-h buffer at the start and end of the cluster windows. Vertical black bars represent GPS fixes, and vertical red bars represent missed GPS fixes. The coloured points are a BCPA time series of VeDBA activity derived from a dual-axis accelerometer at 5-min intervals, with colours from blue-to-yellow corresponding to low-to-high autocorrelation. The band at the top of each cluster identifies the behavioural state (more red equates to higher activity) estimated from *k*-means clustering using the BCPA metrics. Daylight patterns are depicted in grey-shaded bands in the plot background. Cluster 10 is typical of a mule deer fawn (note all daytime fixes), Cluster 16 of a mule deer predation event and Cluster 18 of an elk predation event.

830 m to the north-east. However, we were only able to confirm a single maternal den (Cluster 2; Fig. 3) and rendezvous site (Cluster 5; Fig. 3). Moderately long residency (≥1 week) with a high prevalence of diurnal points and low-to-moderate activity was indicative of den and rendezvous sites (Table S3; Andelt, Althoff & Gipson 1979).

Case 3: territoriality – long-term, low-intensity fidelity

To demonstrate a third utility of the software, we used rASF to identify possible territorial marking sites visited by coyotes for communicating with neighbouring conspecifics. The third data set consisted of coyote relocation data from south-eastern Idaho on the Idaho National Engineering Laboratory during 2005. All individuals were captured using helicopter net-gunning and fitted with Lotek GPS collars (Model 3300S) following the handling protocols outlined in the National Wildlife Research Center QA-1025. Although these collars did not contain directional sensors, they were programmed with 5-min location intervals permitting the estimation of fine-scale, trajectory-based activity data. In this case, we expected infrequent but periodic revisiting of sites by coyotes. Thus, we switched from clustering locations within a time

Table 2. The estimated centroids of all three BCPA statistics, $\hat{\mu}$ (mean of VeDBA), $\hat{\sigma}$ (standard deviation of VeDBA) and $\hat{\tau}$ (time-scale of autocorrelation in VeDBA), for all *k*-means clusters representing four possible behavioural states in cougars and three possible behavioural states in coyotes. The unit for the characteristic time-scale is 5 min, as reflected by the interval of time between activity measurements

	Cougar			Coyote		
Behavioural state	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\tau}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\tau}$
1	6·93	8·53	3·06	80·96	101·72	38·37
2	33·58	39·29	9·57	166·85	88·84	12·90
3	29·39	41·12	28·45	13·01	24·70	6·48
4	81·55	59·06	6·12	–	–	–

interval, as we did for the other two cases, to identifying spatially associated locations that occurred over a longer period of time and that represented revisitation after a predetermined time interval had transpired. We used a minimum number of three fixes and a spatial buffer of 25 or 35 m and clustered only those locations that occurred after 5 days. We selected parameter values to help identify any site with a minimum of three fixes given the short duration of collar deployment (<2·5 months), a small spatial buffer to resolve fine-scale (point) space use while accommodating GPS error and a temporal interval to permit capture of coyote movement patterns within a home range indicative of territorial patrol (≥5 days based on field observations). The number of clusters identified was relatively insensitive to perturbations in all except for the minimum number of fixes (Appendix S1). Further, we anticipated these sites to be associated with intermediate-to-high levels of activity (i.e. non-resting sites) with moderately directed movements (i.e. territorial patrolling). Thus, we integrated activity as we did above, but now by using trajectory-based statistics with persistence velocity as our composite metric in the BCPA. After estimating cluster sites by pack ($N_{\text{Packs}} = 6$, $N_{\text{HRs}} = 12$ across two time periods), we generated concave hulls around the outermost cluster centroids as a representation of territorial boundaries (hereafter denoted territories). We estimated per cent area overlap and median gap distances along shared borders for each concave hull territory using ARCGIS (v.10.2.2; ESRI 2016).

For comparison with more typical home range estimators, we generated pack-specific home range estimates using kernel density in the

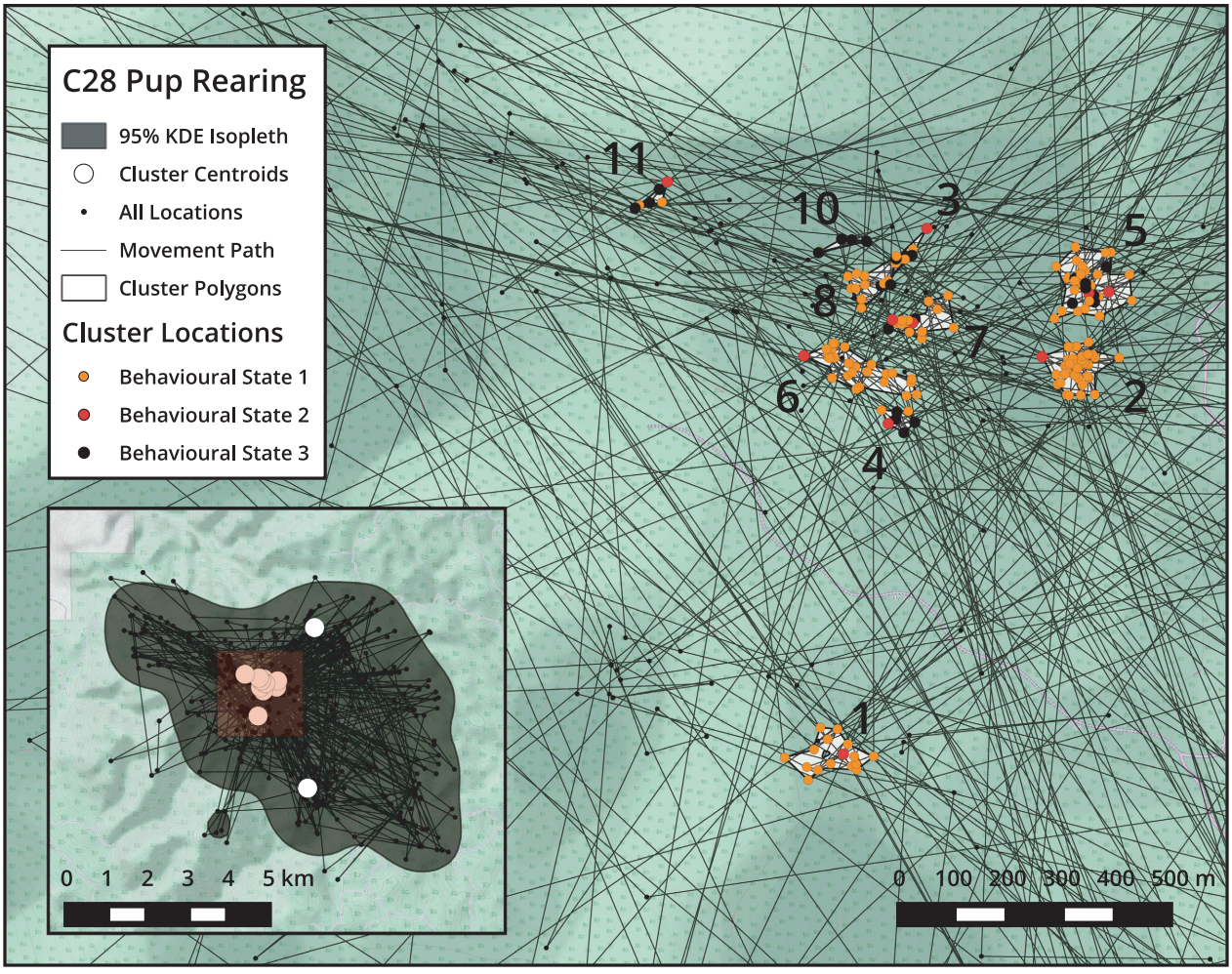

Fig. 3. The points associated with clusters identifying den and rendezvous sites in a high-elevation coyote pack within the Monroe Mountains, Utah. Inset shows the location of the clusters within the pup-rearing seasonal home range. Cluster 1 is the natal den site, cluster 2 is a maternal den site, and clusters 5 and 11 are rendezvous sites. The remaining clusters (3, 4, 6, 7, 8 and 10) represent a combination of possible rendezvous sites that likely depict significant pup movement.

R package *adehabitatHR* (v.0.4.14; Calenge 2006) with an *ad hoc* bandwidth estimator and a bivariate normal kernel. We calculated kernel home range overlap based on per cent area shared between each neighbouring territory as two-dimensional home ranges are often used to estimate availability in resource selection functions. Finally, for each cluster-generated territory, we intersected the concave hull estimates with the pack kernel density rasters using R package *raster* (v.2.5-2; Hijmans 2012) to identify per cent volume encompassed by the concave hulls (i.e. isopleth).

We estimated 10 coyote pack home ranges over two consecutive periods from winter through summer of 2005. Animal locations and home ranges (95–99% KDE) overlapped in all cases where neighbouring packs were monitored. Constraining home range boundaries to the outermost high-fidelity sites as identified by the clustering software reduced perceived home range overlap considerably, from 13·9% (SD = 7; 99% isopleth KDE) to 0·3% (SD = 0·4; concave hull; Tables S4 and S5), while maintaining a median gap distance between territories of 244·5 m (SD = 118·7; Fig. 4; Table S6). Further, 66·9% (SD = 0·21) of the high-fidelity clusters along a shared boundary were visited (≤35 m) by neighbouring conspecifics within the 2- to 3-month period collars were deployed. The territories identified by high-fidelity clusters represented 89·8% (SD = 0·06; Table S7) of the total kernel utilization distribution volume and captured approximately a 90% KDE isopleth, though the home range shapes likely vary in important ways (Fig. S2). Although collared non-resident individuals were rare, one individual was a non-resident for most of the monitoring period and exhibited movements that were largely constrained by the high-fidelity clusters identified (Fig. 5).

Discussion

We demonstrated the utility of our program in identifying sites with high fidelity as determined by user inputs under a number of scenarios. In our first case, we identified predation events by clustering cougar locations in space and time. While spatiotemporal clustering in animal relocation data is commonly used to identify predation events (Anderson & Lindzey 2003; Elbroch & Wittmer 2013; Ebinger *et al.* 2016), few methods are explicitly programmed, incorporate clustering in space and time, or

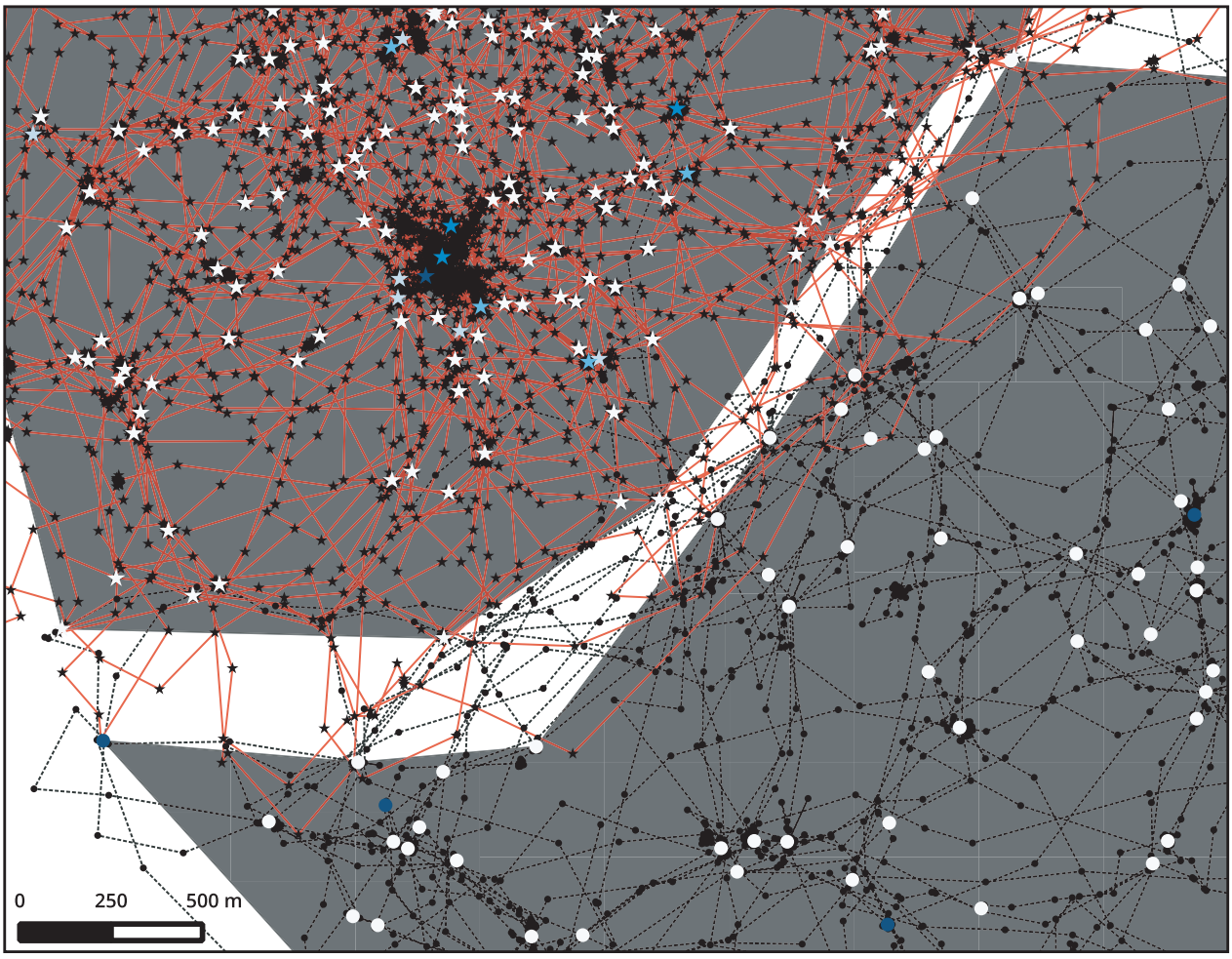

Fig. 4. A boundary between two neighbouring coyote packs at the Idaho National Engineering Laboratory during the winter of 2005, as identified using rASF. The polygons are 100% concave hulls around all active cluster centroids in an effort to capture the boundary in its truest form. The smaller, black stars and circles depict the locations from two neighbouring coyote individuals. The larger icons represent cluster centroids for each individual (stars and circles, respectively; blue ~ least active, white ~ most active). Paths for each individual are included to demonstrate how they move in response to the space use of their neighbour.

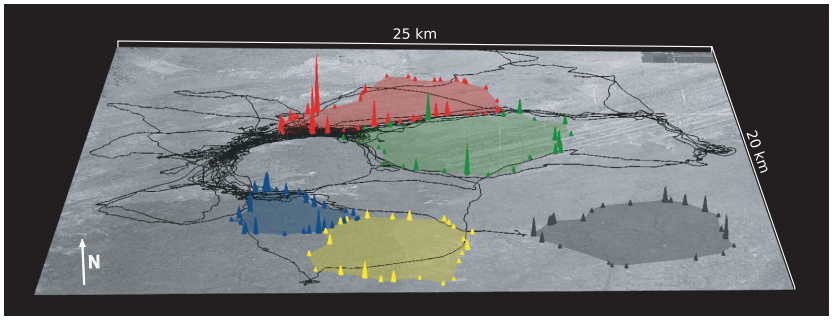

Fig. 5. The path from a single non-resident coyote demonstrating how the individual navigates at least five known, and several suspected, coyote territories during the spring and summer of 2005. Cluster-defined boundaries are depicted as cones with the frequency of revisitation represented by cone height.

provide an efficient and objective means of incorporating activity data. Thus, our method provides a more comprehensive view of a potential predation event by achieving all three components, while providing quick and repeatable output from large quantities of relocation data. However, we caution against visiting potential predation sites based solely on, or even in conjunction with, estimates of behaviour as derived from unsupervised activity. Our recommendation is to visit all or a random subset of clusters to ensure all relevant foraging events are observed during the monitoring period. In cases where researchers rely extensively on activity data during the kill cluster investigation phase, scavenging events might go unobserved while favouring larger prey and in turn significantly under-representing the caloric intake of the individual (Elbroch *et al.* 2014). Provided sufficient quality, resolution and sample size, data gathered during cluster visits, along with cluster-specific metrics (e.g. duration, number of nocturnal fixes), site characteristics and associated activity metrics, can be used to develop predictive models for estimating the probability of kill occurrence and prey type at all remaining unvisited cluster sites.

In our case, we did not have sufficient data to estimate the probability of cougar kill occurrence based on cluster and site metrics. However, rASF performed well at resolving predation events, even of smaller prey species such as beaver and coyote, with 79% of visited clusters containing identifiable kills. We recognize that the detection of carcasses contributed to this number and was likely influenced by prey type, cover class and the time that transpired since a kill occurred (mean = 52·4 weeks, SD = 15·4). Although we did not rigorously assess detection, incidental cluster revisitation by two crews indicated kill detection rate is likely around 80% (n = 5). We had some success predicting individual prey species, particularly mule deer, based on cluster metrics and animal activity using random forest. However, small sample sizes, multiple kills in some clusters (e.g. mule deer doe and fawn or elk cow and calf) and variability in size associated with the 'other' category likely reduced the predictive power in the current assessment. Further, young elk (calves and yearlings) were disproportionately represented in the diet (66·6%) and may overlap with adult deer in terms of biomass, potentially limiting our predictive accuracy in our smaller sample of elk. We attempted to include age class in our random forest response variable, but this resulted in higher out-of-bag error rates and reduced predictive accuracy.

However, should we expect to see differences in activity associated with a variety of prey types?= While the answer is likely system-specific, in our case measures of activity, or VeDBA, also proved informative for distinguishing prey species even after accounting for duration of time spent at a kill (Fig. S1). For context, a kill is often followed by reduced levels of activity and extended periods of autocorrelated movement distinguishable from resting sites and is supported by qualitative assessments of cluster-specific BCPA time series (Fig. 2). Thus, support for variation in activity and the time-scale of autocorrelation before (4 h) and after (8 h) cluster initiation may suggest differences in activity associated with the capture and handling of the two ungulate prey species (Fig. S1). Therefore, we expect that larger sample sizes, added directional sensor resolution (e.g. tri- vs. dual-axial accelerometers, finer temporal measurements) and finer spatial fix rates for better resolution on the timing of a kill will likely improve the predictive accuracy in a predation event context.

In the second scenario, we investigated more intermediate duration and use of locations with high fidelity by identifying den and rendezvous sites (i.e. pup-rearing) from a single male coyote. While using data derived from a breeding female may have been more informative, particularly after she emerges from the natal den and permits GPS satellite acquisition and data transmission, we chose relocation data from a breeding male to demonstrate the efficacy of the method in circumstances where the data may be less clear. In this case, activity and estimates of behavioural state provided additional evidence for the existence of pup-rearing sites. The male's behavioural data indicated low-to-moderate activity with largely daytime visitation at all early- to mid-season sites. This matches our expectations based on knowledge of coyote behaviour where we might anticipate crepuscular or nocturnal foraging by breeding males and other non-breeding pack members with food provisioning for denning females and reduced activity during the daytime while present at pup-rearing sites (Bekoff & Wells 1982). In addition, rASF identified a total of 12 clusters, a number of which were in close proximity to one another and may reflect greater mobility of pups during mid-to-late summer. Thus, based on timing and spatial occurrence, these 12 sites could likely be reduced to six total sites, two den and four rendezvous sites (Table S2). Although the above is intuitive, once the location and timing of these sites have been identified, from here one could investigate other life

history and behavioural metrics such as reproductive phenology, food provisioning rates by males, number of pup-rearing sites and duration of residence at each site as influenced by resource availability, climate change and measures of human disturbance.

In the last case, we demonstrate the utility in identifying sites of long-term, low-intensity use with periodic revisitation by individuals. More specifically, we derived realized territories based on biological patterns associated with potential conspecific signalling and knowledge of scent-marking behaviour in coyotes (i.e. scent marking such as urine, faeces deposition and scratching). And while scent marking along the margins of a territory do not prevent intrusion, they serve to orient individuals in space and most frequently occur at the margins of a territory and in areas with the highest intrusion rates (Wells & Bekoff 1981; Gese & Ruff 1997). Although we did not ground-truth the sites identified by the clustering software as true scent-marking sites in the Idaho population, we believe multiple lines of evidence indicate that these locations effectively demarcate territorial boundaries, including periodic revisitation by individuals within a pack (≤35 m), visitation by neighbouring conspecifics (Gese & Ruff 1997), very little overlap of high-fidelity sites between neighbours along narrow boundary margins (Kamler & Gipson 2000; Wilson & Shivik 2011), moderate- to high-activity levels at nearly all outermost clusters (indicating animals on the move) and a single non-resident individual that exhibited movements largely constrained by these interstitial spaces between territories during the same time period (Kamler & Gipson 2000). While a more rigorous assessment is needed, these results suggest using site fidelity patterns in territorial species could lead to more biologically informed estimates of territory. Further, more explicit assessments of territoriality with respect to conspecific marking in the context of animal space use and movement could lead to an improved understanding of the mechanistic processes leading to home range emergence (Moorcroft, Lewis & Crabtree 2006). Finally, while we focused on establishing the link between patterns in site fidelity, social cues and territorial margins as proof-of-concept, this approach can easily be extended to identify any locations where low intensity of use, but periodic revisitation is expected (e.g. watering sites, social marking sites, mineral acquisition sites).

Only recently has the importance of including behaviour or behavioural state in resource selection been demonstrated (Roever *et al.* 2014). While we do not explicitly address resource selection in the cases described above, one could easily implement our method to quantify the associated landscape features and phenology of behaviours that lead to high levels of fidelity at ecologically important sites. Behaviourally unaffiliated resource selection functions are likely to wash out the importance of low-use sites with significant resource value (i.e. social marking sites). Thus, differentiating these ecologically important sites based on fidelity patterns will permit researchers to explicitly assess selection of low-use sites by means of site-specific characteristics (e.g. scent marking with respect to known movement corridors). Establishing this link will not only improve our predictions of resource selection, but also will be essential to developing our understanding of individual variation in space use behaviour and the fitness consequences of resource selection.

In conclusion, we recognize the field of movement ecology is rapidly evolving, specifically with respect to behavioural classification from animal relocation data. And while we plan to further develop our software to meet the needs of end users and promote more general use of our clustering software by incorporating additional options for behavioural classification (e.g. hidden Markov models, Jonsen *et al.* 2013), the current version provides an efficient, rigorous and repeatable means of identifying site fidelity patterns associated with specific behavioural states. As such, the software has significant potential to inform theory in behavioural ecology while providing managers with better resolution on appropriate management targets associated with key aspects of a species' life history (e.g. Abrahms *et al.* 2016).

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Data accessibility

The GPS and activity data used in this study are available on Movebank (movebank.org, study name: Site fidelity in cougars and coyotes, Utah/Idaho USA) and are published in the Movebank Data Repository with doi:10.5441/001/1.7d8301h2.

R code and a vignette with data sets: GitHub/Zenodo doi:10.5281/zenodo.61429. For most current version, visit https://github.com/PMahoney29/rAnimalSiteFidelity

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Tables S1–S7 and Figs S1–S2. Additional tables and figures containing results relevant to the individual case studies presented, but that were too large or of lesser importance for inclusion in the main manuscript.

Appendix S1. Sensitivity to initial parameters.

Appendix S2. Sensitivity of fine-scale clusters to GPS fix rate and schedules.